

SUBSPECIFIC VARIATION IN THE WIDESPREAD
BURL-FORMING *ARCTOSTAPHYLOS GLANDULOSA*

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ABSTRACT

The genus *Arctostaphylos* consists mostly of chaparral shrubs known by the common name manzanita, and one of the widest ranging of these is *A. glandulosa* Eastw., distributed from Baja California to Oregon. Particularly in the southern half of its range it exhibits complex patterns of morphological variation that have long presented taxonomic challenges. Phenetic analysis of morphological traits from over 1400 individuals from throughout the range were used to examine intra- and inter-population patterns of variation. Multivariate ordination and hierarchical cluster analysis were used to determine phenetic patterns linked with ecological and geographical distributions. These analyses suggest the hypothesis that this species comprises two lineages with a common origin but divergent in the presence or absence of glandularity: *A. glandulosa* Eastw. subsp. *glandulosa*, characterized by branchlets with long glandular hairs, scabrous or pubescent leaves, and nascent inflorescences with mostly foliaceous bracts; and *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey and Parker comb. nov., with non-glandular tomentose branchlets, glabrate or pubescent leaves and either foliaceous or short deltoid bracts. Populations dominated by one or the other of these morphotypes occur throughout the range and tend to be separated by elevation or distance from the coast, although mixed populations occur where these taxa come together.

Two other glandular subspecies are named here. One is *A. glandulosa* Eastw. subsp. *leucophylla* Keeley, Vasey and Parker, subsp. nov., with intensely glaucous leaves and commonly with foliaceous bracts. A second glandular subspecies is *A. glandulosa* Eastw. subsp. *atumescens* Keeley, Vasey & Parker, subsp. nov., a narrowly distributed Baja California endemic similar to the nominate subspecies except that it lacks a basal burl and does not resprout after fire.

Of the non-glandular tomentose taxa, in addition to *A. glandulosa* subsp. *cushingiana*, several others are also recognized. One is *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells, a well established coastal San Diego endemic recognized by darker and thicker leaves and smaller and flatter fruits. Another is a newly described taxon *A. glandulosa* Eastw. subsp. *erecta* Keeley, Vasey & Parker, subsp. nov., an endemic to northern Baja California recognized by the erect nascent inflorescences. Two others have glabrate leaves and highly reduced deltoid often marcescent bracts; *A. glandulosa* subsp. *adamsii* (Munz) Wells, which has intensely glaucous leaves and is distributed from interior Riverside Co. south, and *A. glandulosa* Eastw. subsp. *gabrielensis* (Wells) Keeley, Vasey and Parker comb. nov., which has bright lustrous green leaves and greater fusion of nutlets, and is distributed from the interior San Gabriel Mountains of Los Angeles Co. north to the Sierra Madre Mountains of Santa Barbara Co. All non-glandular plants with long setose or villous hairs are *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells. This taxon includes plants with foliaceous as well as reduced bracts and is distributed throughout the Transverse Ranges from Santa Barbara to San Bernardino counties, with some outlying populations further south. This taxon shows a marked tendency for reduced stomatal densities on the upper leaf surface in the westernmost populations. Although all of the *A. glandulosa* taxa described here are known from allopatric populations, intergradations of these closely related taxa occur and thus some populations reflect a mixture of traits and can not be assigned a unique name of practical value.

Key Words: chaparral, evolution, hybridization, introgression, latitude, subspecies, traits.

Arctostaphylos is a genus of shrubs whose center of diversity is in chaparral shrublands of the California floristic province. Currently 61 species and an additional 32 subspecies are recognized (Wells 2000a). Complex patterns of variation in this genus have been a challenge to taxonomists for more than a century. A number

of factors contribute to this complexity. No fertility barriers are known between species in the genus and hybridization and introgression are suspected to occur between many species. There also is much infra-specific variation that has been treated in various ways, including varieties, subspecies, and forms.

One of the key life history differences between *Arctostaphylos* taxa is the response to fire and this has played an important role in the taxonomy of the genus. High intensity crown fires are a predictable feature of chaparral shrublands and most species in the genus produce dormant seed banks that are stimulated to germinate by chemicals from combustion products of fire (Keeley 1991). Some *Arctostaphylos* species are killed outright by fire and are entirely dependent on seed bank storage (Parker and Kelly 1989) and postfire germination in order to persist in fire-prone environments, and are known as obligate seeders (Keeley 1991). Other species couple postfire seedling recruitment with resprouting from a swollen burl or lignotuber at the base of the main stem (Fig. 1a), and these are known as facultative seeders. These burls, which are an important taxonomic character, are a normal ontogenetic stage and are apparent in seedlings after the first year (Fig. 1b). They potentially confer great longevity to genets capable of persisting through repeated fire cycles and expanding to form platform burls (Fig. 1c) and are an important taxonomic character.

The most widespread Californian *Arctostaphylos* species is the resprouting *A. glandulosa* Eastw. It is common in the coastal mountains from northern Baja California to southern Oregon but is absent from the Sierra Nevada. It is normally circumscribed as a tetraploid ($n = 26$) burl-forming species having isofacial leaves with roughly similar stomatal density on the upper and lower leaf surfaces, and small somewhat depressed globose fruits that comprise half a dozen nutlets variously fused and usually breaking apart into 2–5 segments. The species always possess some form of indument from puberulent to densely glandular hairy. Nascent inflorescence bracts range from linear foliaceous to highly reduced scale-like deltoid.

A number of factors have contributed to patterns of variation in *A. glandulosa*. The widespread distribution in diverse habitats has likely played some selective role in generating variation. Also, the burl-forming habit contributes to patterns of variation not generally seen in obligate seeding species. That is, obligate seeding species mix genes every fire-initiated generation and thus tend to homogenize population characteristics, whereas resprouting allows different morphotypes to persist indefinitely as clones, and thus increase morphological variation within populations. Also the burl forming habit may carry a cost in terms of migration during the marked climatic fluctuations, most recently during the late Quaternary (Axelrod 1950; Raven and Axelrod 1978; Wells 2000b; Rhode 2002), but the effect on patterns of variation are unexplored. Another potential factor is hybridization and introgression. Wells (2000a) specu-

lated that *A. glandulosa* had hybridized with more than a dozen other species, although little morphological or molecular data exist to support this claim.

The most recent treatment of intra-specific variation in *A. glandulosa* is Wells (2000a), which is little changed from Wells (1987). There are a number of features of his treatment that we believe can be improved. Wells' classification relied on induction rather than quantitative analysis. Although he claimed that he had examined a large array of phenetic traits, none of these data were presented in support of his treatment of this or most other species. In addition, he was not a prolific collector and seldom made extensive collections of populations and provided no quantitative comparisons of the range of variability between populations or between subspecific taxa. We have focused in this paper on a quantitative examination of population variation for a large array of phenetic traits, and on populations distributed throughout the range of *A. glandulosa*. Also Wells relied heavily on herbarium material deposited as part of general collections, mostly collected in the spring and thus lacking fruits. As a consequence no mention of fruit characteristics appear in his treatment of subspecific variation in *A. glandulosa*. There are clear examples where this has resulted in substantial errors; e.g., all burl forming *Arctostaphylos* in the Santa Rosa Mountains of Riverside Co., were treated as *A. glandulosa* Eastw. subsp. *adamsii* (Wells 2000a, and unannotated specimens at RSA; see also Munz 1958), but as shown by Keeley et al. (1997a) these plants all possess ovoid apiculate single stone fruits, clearly eliminating any close affinity to *A. glandulosa*; these have been described as *A. parryana* Lemmon subsp. *deserticum* Keeley, Boykin & Massihi.

One of the characteristics of *A. glandulosa* that makes this species taxonomically challenging is that many of the subspecies, which typically form spatially defined allopatric populations of apparently true-breeding forms, occasionally merge in populations that contain mixtures of traits. Wells attempted to recognize these as taxonomic entities by naming 'formas.' These formas could dominate a population or occur as multiple morphs within the same population. We have not used this level of treatment because it is not clear that these 'formas' have phylogenetic significance; i.e., an occasional variant such as an eglandular morphotype within an otherwise glandular taxon may have very different origins across the subspecies' distribution. These 'formas' reflect a fundamental difference between Wells' treatment and that proposed here. He was intent on providing a name for every morphotype present in a population. Our approach is to recognize populations of distinct morphotypes that represent nodes of variation with geograph-



FIG. 1. a) *Arctostaphylos glandulosa* platform-like burl from Mt. Tamalpais, Marin Co; b) young plants with developing burl; c) recently burned platform burl from repeated fire cycles with resprouts at the lower right edge (photographs by J. Keeley).

ically defined distributions. Where these subspecies merge and form mixed populations we recognize these populations as potentially important evolutionary stages but have not attempted to provide names for each morphotype in such populations.

The purpose of the present paper is to investigate patterns of phenetic variation at the intra- and inter-population level for *A. glandulosa*. We have collected several thousand specimens in roughly 80 or more populations from throughout the species' range and recorded 52 characters for each specimen. We examine patterns of phenetic variation in the species and how different populations cluster in phenetic space as a first step to generating a taxonomy of the subspecific variation. We begin by examining a taxon, *A. campbellae* Eastw., that has previously been considered a subspecies of *A. glandulosa* but was removed by Wells (2000a). We then examine the extent to which populations can be characterized as glandular versus non-glandular forms, the latter previously being treated as *A. cushingiana* Eastw. Based on this analysis we recognize three phenetic groups distinguished by differences in branchlet indument, and examine other patterns of subdivision within each of these groups. Our focus throughout is to evaluate how previous taxonomic treatments are supported with this data set.

TAXONOMIC HISTORY

Alice Eastwood (1897) named *A. glandulosa* Eastw. from a specimen on Mt. Tamalpais in Marin Co., California. It was recognized by its long glandular hairs on branchlets and rachises and ability to "stump-sprout" from basal burls and was known to be widely distributed throughout California.

A. cushingiana

Later Eastwood (1933) also named a non-glandular pubescent burl-forming *Arctostaphylos* from lower elevations on Mt. Tamalpais, *A. cushingiana* Eastw. However, Adams (1940) recognized that these two stump-sprouting taxa, *A. glandulosa* and *A. cushingiana*, shared a number of important traits (isofacial leaves, mostly foliaceous lower bracts, and depressed oval fruits with separable nutlets), and he subsumed the latter taxon in *A. glandulosa* with the combination, *A. glandulosa* Eastw. var. *cushingiana* Adams ex McMinn (first treated in McMinn 1939).

For a long time the non-glandular but pubescent "*cushingiana*" taxon was thought to be highly restricted in range. Adams (1940) indicated it was only in the counties north of San Francisco Bay, but Munz (1968) extended its distribution further south to Monterey Co., and Hoover (1970) to San Luis Obispo Co. Our

studies presented here demonstrate it is also present throughout southern California and northern Baja California.

Throughout the last half of the twentieth century there has been much controversy over how to best treat these glandular and non-glandular burl-forming manzanitas. Wells (1968) did not recognize either *A. cushingiana* or *A. glandulosa* var. *cushingiana*, and considered the non-glandular "*cushingiana*" to be nothing more than an intra-population morph that did not occur in allopatric populations apart from glandular-haired plants. In stark contrast, Hoover (1970) considered it a valid taxon and even treated *A. cushingiana* at the species level, noting it was the dominant resprouting manzanita, and that it occurred in pure (i.e., entirely non-glandular) populations over the eastern half of San Luis Obispo Co. He justified treating *A. cushingiana* at the species level because in his view, where *A. cushingiana* and *A. glandulosa* were sympatric, the degree of hybridization was no greater than between other well established *Arctostaphylos* species. Howell (1970) as well believed *A. cushingiana* should be given species status and considered it to be widespread in Marin Co. and quite distinct from *A. glandulosa*, both of which occurred in pure allopatric populations.

In a later publication Wells (1987) acknowledged that the non-glandular "*cushingiana*" taxon did form pure allopatric populations, but in his inimical contrary style reiterated his conviction that it should not be recognized as anything more than an intra-population morph. He justified this on the basis that these allopatric populations of "*cushingiana*" were "local populations" that had a similar range as the nominate form of *A. glandulosa* and therefore would be inappropriately treated as a subspecies. We note that this rationale is inconsistently applied to other taxa in Wells (2000a). Wells' taxon *A. glandulosa* subsp. *zacaensis* (Eastw.) Wells was described as having a distribution that overlapped and co-occurred with other *A. glandulosa* subspecies throughout central and southern California. Also, Wells' dismissal of "*cushingiana*" because it comprised only "local populations" is never explained; as an aside, he generally used that term in a pejorative sense and applied it to several taxa he chose not to recognize, but others such as *A. gabrielensis* Wells, which comprises a small handful of plants from Mill Creek Summit in the San Gabriel Mountains, he described as "narrowly endemic," and never as a "local population."

A. glandulosa var. *crassifolia*

Jepson (1922) named a new variety from coastal San Diego Co., *A. glandulosa* Eastw. var. *crassifolia* Jepson, recognized only by its coastal distribution and thick elliptic leaves, but

this taxon was not recognized by Eastwood (1934). Later Jepson (1925) transferred this taxon, renaming it *A. tomentosa* (Pursh) Lindley var. *crassifolia* (Jepson) Jepson, and later claimed the original placement in *A. glandulosa* was a calamitous typographical error (Jepson 1939, p. 47). In this later publication he further defined the range of variability for this taxon as tomentose and without long hairs. Adams (1940), however retained *A. glandulosa* var. *crassifolia* and expanded the definition of this taxon to include non-glandular tomentose branchlets with dark green leaves, and occasional individuals with longer hairs. He also expanded the distribution to include Baja California. Wells (1968) elevated it to subspecies *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells and later (Wells 1987) justified this based on its allopatric and narrow geographic distribution relative to other morphological types. Wiggins (1980) made an important observation when he noted that the fruits were much wider than tall (consistent with our results presented below) and indicated this taxon was present in northern Baja California. Later Wells (1987) expanded the definition of this taxon to include populations in which 50% of the individuals had long villous hairs, and he gave the range as from Oceanside in San Diego Co. to Cabo Colonett in Baja California. He also considered the range of this taxon to be restricted to coastal outcrops of Eocene age siliceous sandstone. Knight (1981) expanded the distribution of this taxon to include other substrates and further inland (> 10 km from the coast, e.g., Mt. Whitney near Escondido), thus including populations that were substantively different from the type in that they included ones with glandular hairs not unlike the nominate form. As a consequence he concluded that the taxon *A. glandulosa* subsp. *crassifolia* had no validity and was the product of hybridization of *A. glandulosa* with other manzanitas in the area; however presently there are no other *Arctostaphylos* species this close to the coast in San Diego Co. Knight (1981) also reported non-burl forming individuals in the Encinitas population of this taxon, but field observations (Keeley unpublished data) revealed that all such individuals were from layered branches that had rooted and in many instances still maintained connections with burl forming plants.

A. campbellae

Eastwood (1933) named *A. campbellae* Eastw. as a non-glandular tomentose species, separated from *A. cushingiana* by its branchlets with long spreading hairs, present on Mt. Hamilton, Santa Clara Co. She made no mention of it being a sprouting species, but Adams (1940) noted the enlarged root crown as one of the reasons for

subsuming it as *A. glandulosa* Eastw. var. *campbellae* (Eastw.) Adams. He also extended the range to include the lower foothills to the east of Mt. Hamilton in San Antonio Valley, Santa Clara Co. McMinn (1939), apparently lumping it with plants we now recognize as *A. glandulosa* subsp. *mollis* (see below), considered *A. glandulosa* subsp. *campbellae* to be very widely distributed, including the Santa Ynez and San Gabriel Mountains in southern California Transverse Ranges. Hoover (1970) concurred that this variety occurred outside of Santa Clara Co. and noted locations in San Luis Obispo Co. Wells (1987), however, disputed the relationship between *A. campbellae* and *A. glandulosa* and contended that the type population on Mt. Hamilton was a hybrid swarm between *A. crustacea* Eastw. (which he treated as *A. tomentosa* (Pursh) Lindley subsp. *crustacea* (Eastw.) Wells) and *A. glauca* Lindley, and he did not consider the *A. campbellae* taxon to have a close relationship to *A. glandulosa*.

A. zacaensis

In 1933 Eastwood named *A. zacaensis* Eastw., a burl-forming species with pale leaves and glandular hairs from the slopes surrounding Zaca Lake in Santa Barbara Co. Later, Eastwood (1934) suggested this taxon occurred south in San Diego Co. and McMinn (1939) concurred with this range, but followed Adams' (1940) treatment of these plants as *A. glandulosa* Eastw. var. *zacaensis* (Eastw.) Adams. Subsequently, Wells (1968) changed this taxon to *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells and considered it the appropriate name for all *A. glandulosa* lacking eglandular setose hairs, but with foliaceous bracts and any degree of glaucous foliage (Wells 1987). He believed this subspecies did not occur north of Santa Cruz Co. and that it displaced the nominate subspecies south of San Francisco. Additionally, it could occur sympatrically with other subspecies such as *A. glandulosa* subsp. *crassifolia* (Wells 1987) and *A. glandulosa* subsp. *adamsii* (annotation labels on *Munz & Balls 17941*, RSA).

A. howellii

Also in 1933, Eastwood named *A. howellii* Eastw., a Monterey Co. pubescent taxon much like *A. cushingiana* but with glandular rachises. McMinn (1939) added that it had glandular fruits. This taxon was recombined as *A. glandulosa* Eastw. var. *howellii* Adams ex McMinn (McMinn 1939) and later *A. glandulosa* Eastw. subsp. *howellii* (Wells 1968). Hoover (1970) suggested this taxon was "an apparent intergrade" between *A. glandulosa* and *A. cushingiana* and did not formally recognize it. In later treatments, Wells (1987, 2000a) also did not formally recognize this taxon and considered it to be a morphological form of *A. glandulosa* subsp. *zacaensis*.

A. glandulosa var. *mollis* and *A. glandulosa* subsp. *glaucomollis*

Adams (1940) named a non-glandular puberulent form with long setose hairs and foliaceous bracts *A. glandulosa* Eastw. var. *mollis* Adams, based on specimens from La Cumbre Peak in the Santa Ynez Range of Santa Barbara Co. Munz (1959) expanded the circumscription of this taxon to include deltoid-shaped upper bracts and expanded the distribution northward to San Luis Obispo Co. and southward to Riverside Co. Wells (1968) changed the subspecific classification with the recombination, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells. Later he named *A. glandulosa* Eastw. subsp. *glaucomollis* Wells (1987), another non-glandular form with setose hairs separated from *A. glandulosa* subsp. *mollis* by having reduced upper bracts. Wells considered the more foliaceous-bracted subsp. *mollis* to be restricted to the western end of the Transverse Ranges and the reduced-bracted subsp. *glaucomollis* to be restricted to the central and eastern Transverse Ranges.

A. glandulosa var. *adamsii*

Another non-glandular pubescent form from interior San Diego and Riverside counties was named by Munz (1958) as *A. glandulosa* Eastw. var. *adamsii* Munz. It was recognized by the intensely glaucous leaves and highly reduced deltoid bracts and lack of glandular hairs. Subsequently, Munz (1974) treated this as a subspecies. Wells (1987) expanded the definition of this taxon to include densely glandular forms as well as the non-glandular tomentose forms in the type population, and commented that this was the most common form, a detail that, in his words, Munz had "either overlooked or ignored." Later Wells (2000a) further expanded the definition, not only of this taxon, but of the species *A. glandulosa*, by including populations with glabrous branchlets, which justified his subsuming the newly described *A. incognita* Keeley, Massihi and Delgadillo (1997b) into *A. glandulosa* subsp. *adamsii*.

A. gabrielensis

On a brief field trip led by the senior author (JEK), Phil Wells collected a few specimens from a roadside population at Mill Creek Summit in the San Gabriel Mountains and named *A. gabrielensis* Wells (Wells 1992), a taxon he suggested had similarities to four other species of *Arctostaphylos*, but *A. glandulosa* was not one of them. However, later Wells (2000a) reversed this opinion and concluded that *A. gabrielensis* was actually a hybrid between *A. glandulosa* and *A. parryana* Lemmon. Wells considered the combination of a resprouting population with single stone fruits resulting from cohesion of

endocarp segments to represent a unique combination and worthy of recognition at the species level. However, his lack of population-level study of the Mill Creek Summit population misled him because the solid stones of fused endocarp drupelets present in the type specimen (Wells and Keeley 31086 CAS), as will be shown below, are an uncommon trait in this population. Also, the phenetic analysis presented here will show that *A. gabrielensis* falls well within the range of variation for *A. glandulosa* in the interior portions of the San Gabriel Mountain Range.

Other Taxa

Adams (1940) named several other varieties of *A. glandulosa*. One of these, *A. glandulosa* var. *australis* Adams from southwestern San Diego Co., was based mostly on leaf shape characteristics. Munz (1959), who followed most of Adams' treatment for *Arctostaphylos*, did not recognize this variety, and Wells (1987) considered this a form of *A. glandulosa* subsp. *zacaensis*.

Other taxa associated with *A. glandulosa* at one time or another include the following. *Arctostaphylos glandulosa* var. *vestita* (Eastw.) Jepson (1922) has been considered to be *A. tomentosa* (Pursh) Lindley in all subsequent treatments because the bifacial leaves separate it from the isofacial leaves of *A. glandulosa*. Also, *A. glandulosa* var. *virgata* (Eastw.) Jepson (1922) was named from Mt Tamalpais, but subsequent authors have noted the lack of a basal burl and treated this taxon as *A. virgata* Eastw. Wells (2000a) considered *A. virgata* to be substantially different from *A. glandulosa* in a number of leaf and bract characteristics and placed in a separate subsection.

METHODS

Several thousand herbarium specimens of *A. glandulosa* and related taxa were collected by the lead author (JEK) and students over a period of several years and deposited at RSA. It was not logistically feasible to systematically collect equally from all parts of the vast range of this species. We made inferences about where collections were likely to be most informative. The information that most influenced our collecting sites were: (i) prior knowledge of variation not clearly accounted for by past taxonomic treatments, (ii) areas occupied by previously described subspecies, and (iii) regions where there had not been much prior collecting. Since 5 of the 6 recognized subspecies in Hickman (1993) are southern California endemics, collecting was concentrated in the southern half of the state. Because Baja California had been poorly studied, further concentration was given to that region as well. Collections were restricted to late summer

TABLE 1. MORPHOLOGICAL TRAITS SCORED OR CALCULATED FOR *A. GLANDULOSA* SPECIMENS. Not all of these traits are informative about intraspecific variation in this species but have been included as part of a larger study of trait variation in the genus.

Burl	no burl = 1, burl = 5
Leaves	
Blade length	measured (mm)
Blade width	measured (mm)
Length/width	calculated ratio
Petiole length (mm)	measured (mm)
Blade basal angle	measured (°)
Blade apical angle	measured (°)
Stomata (adaxial surface)	density
Stomata (abaxial surface)	density
Stomatal ratio	adaxial density/abaxial density
Color	1 = yellow, 3 = yellow-green, 5 = green
Luster	1 = glaucous, 3 = intermediate, 5 = glossy
Scabrous	1 = smooth, 3 = intermediate, 5 = scabrous
Indument pubescence	1 = glabrous, 2-3 = short pubescences, 4-5 = long hairs
Scored for branchlets, old leaves, new leaves, rachises, pedicels, and fruits separately	
Indument glandularity	1 = glabrous, 2-3 = viscid glands, 4-5 = long glandular hairs
Scored for branchlets, old leaves, new leaves, rachises, pedicels, and fruits separately	
Nascent inflorescence	
Orientation	1 = descending, 3 = ascending, 5 = erect
Bract spacing	1 = overlap to 5 = well spaced
Bract keel	1 = no, 3 = moderate, 5 = deeply keeled
Bract shape	1 = lanceolate, 3 = deltoid-acuminate, 5 = ovate
Bract tip marcescent	1 = no, 5 = yes
Bract reflexed	1 = no, 5 = yes
Bract length (lower)	measured (mm)
Bract length (upper)	measured (mm)
# of rachis branches	
Fruiting inflorescence	
Rachis length	measured (mm)
Pedicel length	measured (mm)
Sepal shape	1 = obtuse, 5 = acuminate
Sepals reflexed	1 = no, 5 = yes
Fruits	
Color	1 = tan, 2 = orange, 3 = red, 4 = brown, 5 = purple
Height	measured (mm)
Width	measured (mm)
Width/height	calculated ratio
Mass of entire fruit	measured (g)
Mesocarp	1 = mealy, 3 = leathery, 5 = papery
Mass of endocarp	measured (g)
# of endocarp segments	measured (g)
Endocarp height	measured (mm)
Endocarp width	measured (mm)
Endocarp width/height	calculated ratio
Endocarp apiculate	1 = no, 5 = yes
Endocarp ridges	1 = no, 5 = yes
Endocarp sculpturing	1 = no, 5 = yes

or fall in order to increase the chances of obtaining specimens with both mature fruits and nascent inflorescences, both of which are key characters in *Arctostaphylos* taxonomy and far more critical in most cases than flowers. When possible, population samples of 15-30 or more individuals were collected. Dried specimens that possessed both fruits and nascent were

scored for 48 (23 vegetative and 25 reproductive) traits and 4 other traits were calculated (Table 1). Stomatal density was determined from clear nail polish impressions that were peeled off leaves, mounted on glass slides and viewed at 40× with a compound microscope.

Eighty populations were sampled, but those with fewer than 5 individuals were eliminated

from further analysis, leaving a total of 1342 plants distributed across 69 populations. The average score for each trait was calculated for each population.

Our initial analysis of all *A. glandulosa* populations included all characters in a multivariate analysis using PC-ORD (McCune and Mefford 1999). Nonmetric multidimensional scaling (NMS), Principal Components Analysis and Reciprocal Averaging were used to examine relationships among the populations. Character scores were relativized to range between 0 and 1.0 to prevent weighting of characters.

For our initial analysis of the relationship of *A. campbellae* to *A. glandulosa*, and for other intra-specific analysis we used cluster analysis. Using the population by trait data matrix, all variables were standardized as z-scores by subtracting the variable sample mean from each value and then dividing the difference by the sample standard deviation. This data matrix was used in the Hierarchical Cluster procedure that calculated normalized Euclidean distance (root mean squared distances) and expressed the results as dendrograms with distance metrics. Traits selected were those generally considered important in separating infra-specific taxa in *A. glandulosa*. In order to avoid overly weighting certain types of characters, traits that exhibited high colinearity, as shown with least squares regression, were avoided. Traits were removed if they did not greatly contribute to the initial cluster pattern. Thus, generally most analyses included only 1 or 2 traits from the following trait classes: leaf color and shape, indument, inflorescence bracts, and fruits. The primary criterion for whether or not a cluster was relevant to our study of subspecific variation patterns was if clustered populations shared similar geographical and ecological situations. Where group comparisons were made, this was with Kruskal-Wallis test using population mean values. All analyses other than the multivariate analyses described in the previous paragraph, utilized the SYSTAT 11 statistics software (www.systat.com).

RESULTS

Evaluating the Inclusion of *A. campbellae*

In order to make a decision as to whether or not the taxon originally described as *A. campbellae* should be included in this treatment of *A. glandulosa* we made the following comparison. The type population on Mt. Hamilton (Santa Clara Co.), and a couple similar populations from San Antonio Valley (Santa Clara Co.) just to the east of Mt. Hamilton, all treated by Adams (1940) as *A. glandulosa* var. *campbellae*, were compared with three species previous authors suggested had close affinities: *A. crustacea*, *A.*

glandulosa, and *A. glauca*. The *A. glandulosa* population was from the type locality (La Cumbre Peak) of *A. glandulosa* subsp. *mollis*, chosen for comparison because it exhibits several features in common with *A. campbellae*, including branches that are non-glandular and pubescent with long setose hairs. *Arctostaphylos crustacea* is also non-glandular with long setose hairs but is distinguished from *A. glandulosa* in having bifacial leaves in which the upper leaf surface is astomatous, in contrast to the isofacial leaves of *A. glandulosa* that are considered to have similar stomatal densities on both surfaces (Howell 1945). *Arctostaphylos glauca* was included because Wells (2000a) considered *A. campbellae* a hybrid between *A. crustacea* and *A. glauca*.

In light of these differences, one of the first characters to assess was stomatal distribution (Table 2). As expected, our population of *A. crustacea* lacked stomata on the upper leaf surface, and our *A. glandulosa* population had many stomata on the upper leaf surface, however, surprisingly this population of *A. glandulosa* subsp. *mollis* had only 37% as many stomata on the upper surface as the lower surface. The *A. campbellae* populations were between these two extremes: 6, 15, and 23% for the Mt. Hamilton, southern San Antonio and northern San Antonio populations, respectively. *Arctostaphylos glauca* stomata were evenly distributed on both surfaces and the density was greater than on any of the other taxa.

The cluster analysis was based on 10 vegetative traits and 12 reproductive traits (Fig. 2). It indicated that the *A. campbellae* populations were morphologically closer to *A. crustacea*, but both of these taxa were much more closely aligned with *A. glandulosa* than with *A. glauca*. The *A. campbellae* populations may represent a subspecific variant of *A. crustacea*, recognized by the presence of some stomata on the upper leaf surface, the consistent presence of tomentum on the lower surface, and the rounded to obtuse leaf bases. Regardless, we have not considered *A. campbellae* populations further in this analysis of *A. glandulosa* subspecific variation.

A. glandulosa Population Patterns: Glandular vs Non-Glandular

Because of the long standing difference of opinion on the reality of a non-glandular pubescent "*cushingiana*" taxon distinct from the glandular taxon in *A. glandulosa*, we began by asking whether or not glandular plants were separable in trait space from non-glandular plants. We compared several ordination methods and all produced similar patterns, but only the nonmetric multidimensional scaling (NMS) results are presented (Fig. 3). In this analysis we utilized the entire data matrix of 52 characters

TABLE 2. STOMATAL DISTRIBUTION ON UPPER AND LOWER LEAF SURFACES IN *ARCTOSTAPHYLOS GLANDULOSA* AND ASSOCIATED SPECIES' POPULATIONS.

Taxon population(s)	Leaf stomata	
	Density on lower surface (# / mm ²)	Upper/lower surface ratio
	\bar{X} (range)	\bar{X} (range)
<i>A. crustacea</i>	21.8 (14.6–28.3)	< 0.01
<i>A. campbellae</i>		
Mt. Hamilton	17.9 (13.3–24.8)	0.06 (<0.01–0.26)
Southern San Antonio Valley	21.6 (16.4–33.2)	0.15 (<0.01–0.46)
Northern San Antonio Valley	21.2 (19.6–29.2)	0.23 (0.08–0.35)
<i>A. glandulosa</i>		
subsp. <i>mollis</i> (Munz) Wells	16.8 (10.6–24.3)	0.37 (0.20–0.54)
Group A	27.9 (14.9–32.4)	0.74 (0.52–0.93)
Group B	27.0 (15.6–32.2)	0.77 (0.41–1.02)
Group C	27.8 (16.8–31.8)	0.71 (0.37–0.71)
<i>A. glauca</i>	31.5 (19.6–41.9)	1.0 (0.83–1.7)

and all 69 populations, although five outlier populations were removed from the final analysis. This analysis is presented in Figure 3 with different symbols for three categories: a) glandular (black triangles), b) non-glandular short tomentose (gray squares) and c) non-glandular short tomentose plus long setose hairs (white

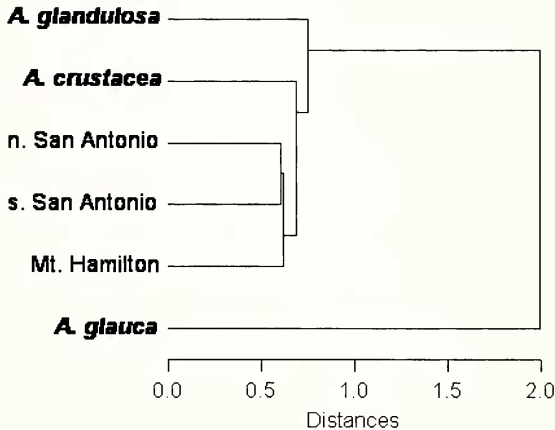


FIG. 2. Hierarchical cluster analysis for of *A. campbellae*, *A. crustacea*, *A. glandulosa* and *A. glauca*. The *A. campbellae* populations were from the type locality (Mt. Hamilton, Santa Clara Co.) and southern and northern ends of the valley east of Mt. Hamilton (n. or s. San Antonio), $n = 19, 15$ and 8 respectively; *A. crustacea* from San Benito Co., $n = 11$; *A. glandulosa* subsp. *mollis* from the type population on La Cumbre Peak, Santa Barbara Co., $n = 13$; *A. glauca* from Los Angeles Co., $n = 35$. Cluster analysis was based on population means for the following leaf traits, length, width/length ratio, basal angle, luster, scabrous, abaxial stomatal density, stomata ad-/abaxial ratio; other vegetative traits, burl, branchlet pubescence; reproductive traits, bract spacing, bract shape, bract reflex, lower bract length, middle bract length, rachis length, fruit color, fruit height, mesocarp, number of stones, apiculate, and fruit width/height ratio.

diamonds). In this analysis most populations designated as glandular sorted out in trait space separate from non-glandular plants. Glandular populations had a population mean score for glandular branchlets (on a scale from 1–5) of 4–5 with the cutoff being 2.9, comprising 26 populations and represented as Group A in subsequent analyses (Table 3). Non-glandular plants were the only or dominant form in over half of the populations, and these made up Groups B and C, dependent on whether or not they possessed long setose hairs (Table 3). Of these, the vast majority were homogenous with respect to lack of glandularity; out of the 43 populations comprising Groups B and C, all but six had a coefficient of variation (CV) for the glandularity index that was 0–50%, indicating relatively limited varia-

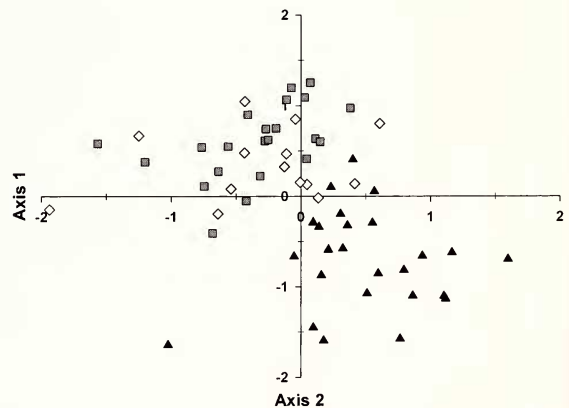


FIG. 3. Nonmetric multidimensional scaling ordination for all characters and all 69 populations, although five outlier populations were removed from the final analysis; populations were classified as glandular (black triangles), non-glandular short tomentose (gray squares) or non-glandular short tomentose plus long setose hairs (white diamonds) as described in Table 3.

tion. Several populations had a CV between 70–78% resulting from a mixture of some glandular plants in an otherwise non-glandular population.

Comparison Between Glandular and Non-Glandular Groups

Subsequent analyses were based on analyzing patterns of variation both between (this section) and within (next section) glandular and non-glandular groups (Table 3). The ordination analysis on all traits clearly separated the glandular from the non-glandular populations, however, within the non-glandular forms the populations with long setose hairs overlapped in trait space with populations lacking such hairs (Fig. 3). We made the decision to weight this trait more heavily than others because setose hair populations occurred in geographically restricted areas with limited overlap with other forms, and because this trait has been weighted heavily in previous taxonomic treatments. Thus, for subsequent analysis we retained the subdivision of non-glandular populations into those without (Group B) and those with setose hairs (Groups C).

Groups were not significantly different in mean latitude of distribution (using the Kruskal-Wallis test), but Group A populations tended to occur at lower elevations and closer to the coast than Group C ($P < 0.01$). In addition to the branchlet glandularity trait on which Group A was based, there were parallel differences in glandularity of other structures; Group A had significantly ($P < 0.001$) greater glandularity for leaves, rachises, pedicels and fruits than Groups B and C. There were five other traits for which Group A exhibited highly significant ($P < 0.001$) differences from both Groups B and C; Group A leaves were much more scabrous, and they had longer rachises, and narrower, less keeled, and less marcescent bracts. Lower bracts in Group A were significantly ($P < 0.001$) longer than in Group B, but Group C was not significantly different from the other two groups in this trait. Group B sepals were significantly more reflexed than Group A and the number of endocarp segments were significantly fewer than in either Groups A or C ($P < 0.05$).

Comparisons Within the Glandular Group A

Cluster analysis of Group A with several different selections of leaf, inflorescence and fruit characters (not shown) failed to uncover any clusters tied to a particular geographical region or ecological habitat. This glandular group did, however, have two variants worth recognizing, each based on a single divergent trait. One was a unique population (A2 Punta Banda lower, Table 3) that lacked basal burls, and observa-

tions in a recently burned area indicated it also failed to resprout. In other vegetative and reproductive traits it was not separable from nearby resprouting glandular populations. Another recognizable variation was a number of populations that had leaves covered with a heavy glaucous bloom. This was explored in greater detail because Wells (1987; 2000a) used this trait to separate non-glaucous northern California *A. glandulosa* Eastw. subsp. *glandulosa* from glaucous central and southern California *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells. Cluster analysis on just leaf luster, color and shape revealed two populations with very intensely glaucous leaves separated clearly from all other populations in this group (populations A3 from Baja California and A16 from San Diego Co., top of Fig. 4). These heavily glaucous plants also tended towards long foliaceous inflorescence bracts. Relative to these two populations, other glandular populations grouped together forming sub-clusters reflecting differing degrees of glaucousness that ranged from somewhat glaucous (A14 and A18, from interior ranges in San Diego and Riverside counties) to largely (A12 and A13) or entirely (A6) non-glaucous populations from more coastal mountains in San Diego Co.

Comparisons Within the Non-Glandular Group B

Cluster analysis of the non-glandular plants in Group B is shown in Fig. 5 based on leaf characters of length/width ratio, color, luster, and pubescence on old leaf blades, nascent inflorescence orientation, sepals reflexed, and fruit characters including mass, width/height ratio and pubescence on the outside pericarp. Population B1 (top of Fig. 5), near the village of La Candelaria in Baja California, exhibited the greatest separation distance and was unique in that most of the plants in the population had erect nascent inflorescences, in contrast to the pendent orientation of all other populations of *A. glandulosa*.

Two other clusters of populations are worth noting because within each cluster are populations in close geographical proximity, plus these clusters match previously described taxa. One of these (B8, B9 and B10, bottom of Fig. 5) comprises populations located along the immediate coast in San Diego Co., and historically has been recognized as *A. glandulosa* Eastw. subsp. *crassifolia* (Jeps.) Wells. This cluster was highly dependent on the inclusion of fruit shape and mass. The average fruit width/height ratio for all populations in this study was 1.3, whereas the three San Diego coastal populations (B8, B9 and B10) ranged from 1.6–1.9, indicating much more flattened fruits than typical for the species. In addition these populations had rather small fruits,

TABLE 3. *ARCTOSTAPHYLOS GLANDULOSA* POPULATIONS USED IN NONMETRIC MULTIDIMENSIONAL SCALING AND HIERARCHICAL CLUSTER ANALYSIS, DIVIDED INTO GLANDULAR AND NON-GLANDULAR POPULATIONS. The latter were further subdivided into those with short canescent or tomentose branchlets and those that also had longer setose hairs. Populations with fewer than 5 specimens were not included, resulting in 1342 individuals distributed between 69 populations. Group A, glandular haired populations typically had branchlet glandularity scored 4-5 (on a scale from 1-5) with the minimum population mean of 2.9. Group B populations lacked long setose hairs unlike Group C populations, which were dominated by plants with long hairs.

Population	County	Latitude	Elevation (m)	Distance (km)	N	
Group A: Glandular hairs						
A1	Punta Banda upper	n. Baja	31°40'	650	3	27
A2	Punta Banda lower	"	31°41'	630	2	18
A3	Cerro Bolo Peak	"	32°19'	1220	30	43
A4	Tecate	San Diego	32°29'	760	44	8
A5	Otay Mtn	"	32°37'	970	28	35
A6	San Miguel Mtn	"	32°43'	310	25	15
A7	Los Pinos	"	32°45'	1270	57	18
A8	Japutal Valley Rd	"	32°49'	1040	53	17
A9	Guatay	"	32°51'	1120	67	5
A10	Escondido	"	33°08'	450	17	35
A11	Carlsbad	"	33°09'	90	5	31
A12	Merriam Mtns	"	33°13'	400	20	36
A13	San Marcos	"	33°13'	445	20	37
A14	Palomar Mtn (east)	"	33°16'	1085	57	18
A15	Palomar Mtn (west)	"	33°20'	1470	49	22
A16	Palomar Mtn (north)	"	33°20'	1470	63	39
A17	Palomar Peak	"	33°22'	1870	61	15
A18	Rancho California	Riverside	33°30'	830	28	8
A19	Red Mtn	"	33°37'	1100	55	10
A20	Blue Jay Camp	Orange	33°45'	1575	70	41
A21	San Jacinto	Riverside	33°46'	1570	70	41
A22	Refugio Pass	Santa Barbara	34°32'	935	12	56
A23	Figueroa Mtn	"	34°45'	1155	46	13
A24	Chews Ridge	Monterey	36°18'	1485	19	15
A25	Mt. Tamalpais	Marin	37°55'	525	4	11
A26	West Point Inn	"	37°55'	500	5	6
Group B: No glandular hairs, indument only tomentose or short canescent						
B1	La Candelaria	n. Baja	31°53'	580	24	42
B2	Tres Aguajes	"	31°55'	490	16	15
B3	Sierra Juarez	"	31°57'	1390	59	17
B4	Cerro Bolo (base)	"	32°19'	700	31	19
B5	El Condor	"	32°29'	1200	125	18
B6	Potrero Peak	San Diego	32°38'	870	50	6
B7	Cottonwood	"	32°47'	1350	78	24
B8	Del Mar	"	32°57'	115	1	6
B9	San Dieguito	"	33°00'	90	4	7
B10	Encinitas	"	33°03'	95	3	21
B11	Glendora Ridge	Los Angeles	34°13'	1410	80	19
B12	Shortcut	"	34°16'	1400	53	10
B13	Windy Gap	"	34°17'	1545	59	11
B14	Chilao	"	34°19'	1600	59	13
B15	Mt Gleason Peak	"	34°22'	1790	52	30
B16	Mt Gleason (base)	"	34°23'	1520	57	11
B17	Mill Creek Summit	"	34°23'	1470	60	20
B18	Pacifico	"	34°23'	1735	61	28
B19	Mt Gleason (midway)	"	34°23'	1670	55	28
B20	Rose Valley	Ventura	34°32'	1150	32	11
B21	Reyes Peak	"	34°38'	2030	37	10
B22	Pine Mtn	"	34°39'	1750	37	21
B23	Bates Canyon	Santa Barbara	34°46'	1375	89	15
B24	Sierra Madre Ridge	"	34°55'	1570	92	47
B25	Black Mtn	San Luis Obispo	35°23'	1080	40	26
B26	Mill Valley	Marin	37°55'	130	7	15
B27	Drakes Hwy	"	38°10'	120	5	10
B28	Mt. St Helena	Sonoma	38°40'	1100	49	16

TABLE 3. CONTINUED.

Population	County	Latitude	Elevation (m)	Distance (km)	<i>N</i>	
Group C: No glandular hairs but longer setose hairs						
C1	Enrendira	n. Baja	31°13'	60	4	15
C2	Kitchen Creek	San Diego	32°48'	1460	71	30
C3	Laguna Mtns	"	32°57'	1615	75	31
C4	Angeles Oaks	San Bernardino	34°08'	1660	104	10
C5	Santa Ana River	"	34°12'	1700	110	22
C6	Seven Oaks	"	34°13'	1920	113	18
C7	Switzers	Los Angeles	34°16'	1070	46	6
C8	Lytte Creek	San Bernardino	34°17'	1595	80	20
C9	Lake Arrowhead	"	34°18'	1580	103	12
C10	Crystal Lake	Los Angeles	34°19'	1720	70	13
C11	La Cumbre Peak	Santa Barbara	34°29'	1185	13	13
C12	Camino Cielo East	"	34°30'	1110	15	7
C13	Liebre Mtns	Los Angeles	34°43'	1670	82	23
C14	Zaca Peak	Santa Barbara	34°47'	1125	51	7
C15	La Cuesta	San Luis Obispo	35°21'	600	22	7

with fruit mass ranging from 100–161 mg whereas the mean for all populations was 251 mg.

A second cluster (B3, B4, B5, and B7, near the top of Fig. 5) included populations, from southeastern San Diego Co. and adjacent Baja California. This cluster was sensitive to the inclusion of leaf and bract traits and these plants were characterized by intensely glaucous leaves and highly reduced bracts, matching closely the original description of *A. glandulosa* Eastw. var. *adamsii* Munz.

Further analysis of Group B was prompted by the fact that one of the populations (B17 Mill Creek Summit, Table 3) was the type locality for *A. gabrielensis* Wells. Cluster analysis was done on the Group B data after removing those populations discussed above, using the characters considered by Wells (1992) as critical in distinguishing *A. gabrielensis* as a new species: leaf color, luster, glabrousness, bract length and number of endocarp segments. In this cluster analysis (Fig. 6) the *A. gabrielensis* population (B17) was clearly embedded within a cluster of other *A. glandulosa* populations (B11, B13, B14, B15, B16, B18, and B19), all of which are located in the interior San Gabriel Mountains (Table 3). A phenetically similar disjunct population (B24, Fig. 6) occurs in the Sierra Madre Mountains of Santa Barbara Co. Morphologically these populations are all recognizable by their glabrous and highly lustrous leaves as well as their reduced bracts and a tendency for endocarp segments to remain consolidated in 1 or 2 segments.

Because Wells (2000a) speculated that *A. gabrielensis* was of hybrid origin between *A. glandulosa* and *A. parryana* Lemmon we did a cluster analysis using 283 specimens from an earlier study of burl-forming populations of *A. parryana* (Keeley et al. 1997a). Using the same traits listed above we found *A. parryana* was close to the cluster of populations in the interior San

Gabriel Mountains (cluster diagram not shown), reflecting the close phenetic similarity between these taxa. Fruit characteristics provide the clearest differences between *A. parryana* from *A. glandulosa* (Table 4). The former species has large solid round endocarp stones with apiculate tips, whereas typical *A. glandulosa* fruits are flattened and break apart into multiple segments. The interior San Gabriel Mountains populations of *A. glandulosa*, including the Mill Creek type population for *A. gabrielensis*, showed a tendency towards certain aspects of *A. parryana* fruits, including the larger size and a tendency for producing some fruits with solid apiculate stones.

Comparisons Within the Non-Glandular Group C

Non-glandular plants with long setose or hispid hairs represented collections that Wells (1987, 2000a) had subdivided into two subspecies, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells and *A. glandulosa* Eastw. subsp. *glaucomollis* Wells. The basis for this separation was the contention that the former had foliaceous bracts and was restricted to the western end of the Transverse Ranges, and the latter had reduced bracts and was restricted to the central and eastern end of the Transverse Ranges. Our initial group comparison did show that both bracts were present in Group C, reflected in our comparison among groups; Group A had significantly longer bracts than Group B, but Group C was not significantly different from either A or B. However, we found no geographical basis for the distribution of bract length in Group C that would support Well's treatment. Cluster analysis using bract length alone (not shown) failed to reveal any geographic clustering, due to the fact that long foliaceous bracts were present in populations throughout the Transverse Ranges.

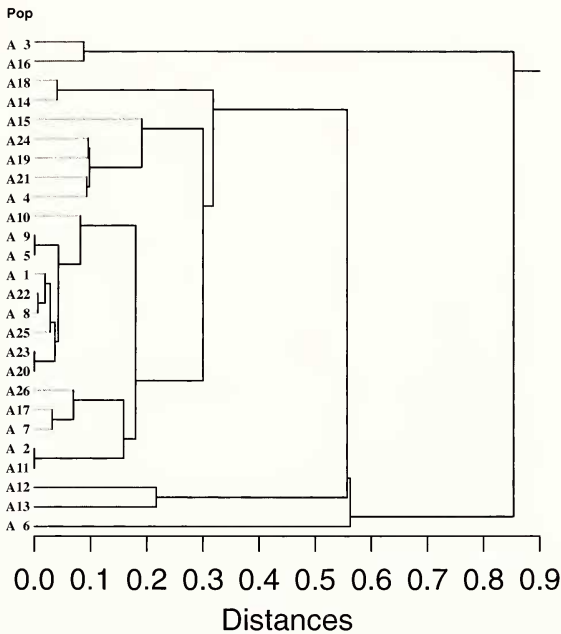


FIG. 4. Cluster analysis for Group A glandular plants for leaf traits, luster, color and length/width ratio. See Table 1 for trait description and Table 3 for population information. Note that populations within a group are arranged by latitude and so the numerical order of populations reflects their proximity to one another.

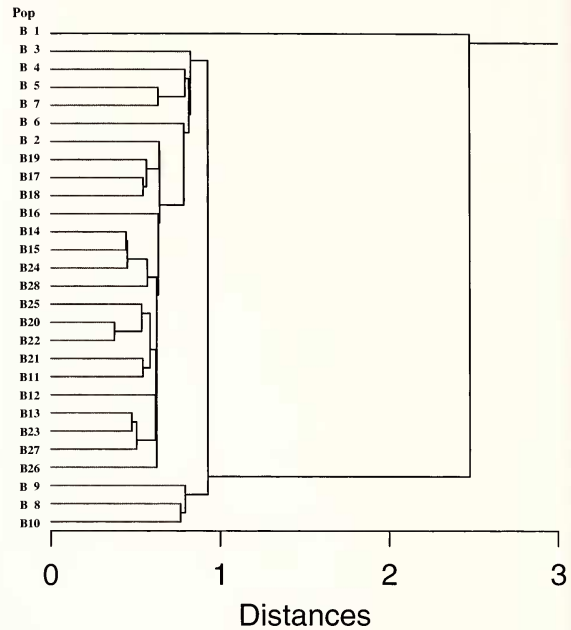


FIG. 5. Cluster analysis for Group B non-glandular plants with tomentose branchlets. Traits included leaf characters of length/width ratio, color, luster, and pubescence on old leaf blades, nascent inflorescence orientation, sepals reflexed, and fruit characters including width/height ratio, pubescence on the outside pericarp, type of mesocarp, and number of endocarp segments. See Table 1 for trait description and Table 3 for population information.

In the study of *A. campbellae* populations reported above it was demonstrated that the type population for *A. glandulosa* subsp. *mollis* from La Cumbre Peak in Santa Barbara Co. had a tendency towards bifacial leaves. This was evident in greatly reduced stomatal density, and greater luster, on the upper leaf surface. Comparison of stomatal patterns for this population with other averages for the three *A. glandulosa* groups (Table 2) revealed the surprising result that very few *A. glandulosa* populations had equal densities of stomata on both leaf surfaces as suggested by Howell (1945). On average Groups A, B and C all had about 25% fewer stomata on the upper leaf surface, although there was a great deal of variation within each group. The type population for *A. glandulosa* subsp. *mollis* had the lowest ratio for all *A. glandulosa* populations, but the ranges shown in Table 2 reveal that there are populations in the other groups that come close in having substantially fewer stomata on the upper leaf surface. Regression analysis showed that the ratio of upper/lower leaf surface stomata was correlated with environmental patterns; e.g., it was negatively related to latitude and positively tied to elevation and distance from the coast ($P < 0.05$).

The cluster analysis of Group C was repeated including stomatal characters along with other

leaf and bract characters (Fig. 7). This analysis showed that the type population for *A. glandulosa* subsp. *mollis* (C11, top of Fig. 7) was somewhat distinct from the other Group C populations. The next closest population (C13) was also from the western Transverse Ranges and in both cases these were populations with relatively low stomatal ratios. Other populations (C12, C14, and C15) from the western end of the Transverse Ranges had phenetic patterns not too dissimilar to populations in the eastern end of range. Thus, other than a tendency for reduced stomatal density on the upper leaf surface in some populations from the western end of the Transverse Ranges, this analysis does not support any strong geographical association with leaf or bract traits.

Finally, several of the Group C populations were mixtures of plants with and without these long hairs. These mixed populations included a couple in the Transverse Ranges — Seven Oaks (C6) in the San Bernardino Mountains and Crystal Lake (C10) in the San Gabriel Mountains — as well as a few populations outside of the Transverse Ranges, including Erendira (C1) in northern Baja California, Kitchen Creek (C2) and Laguna Mountains (C4) in San Diego Co.

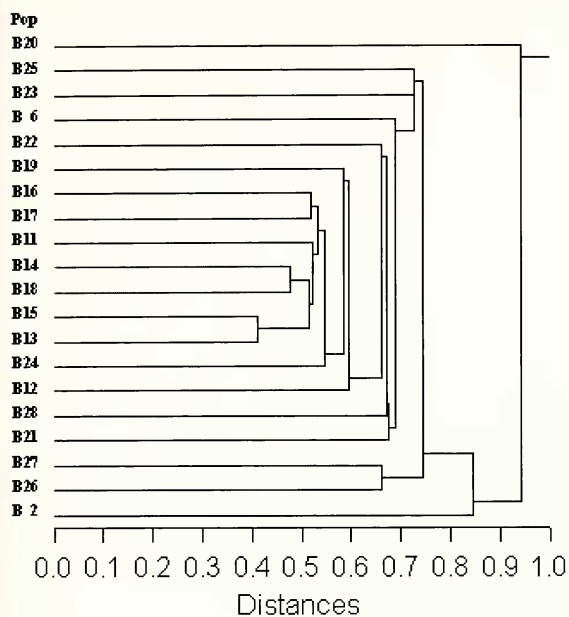


FIG. 6. Cluster analysis for Group **B** non-glandular plants with tomentose branchlets but with the three clusters represented in Figure 5 by populations 1, and 3, 4, 5, 7, and 8, 9, 10 removed. Analysis of remaining populations in Group **B** were with leaf characters of length/width ratio, color, luster, lower bract length, sepals reflexed, and fruit characters including width/height ratio, type of mesocarp, and number of endocarp segments. See Table 1 for trait description and Table 3 for populations described by the case numbers.

TAXONOMIC TREATMENT

We hypothesize that glandular and non-glandular tomentose populations are two lineages that occur throughout the coastal ranges of

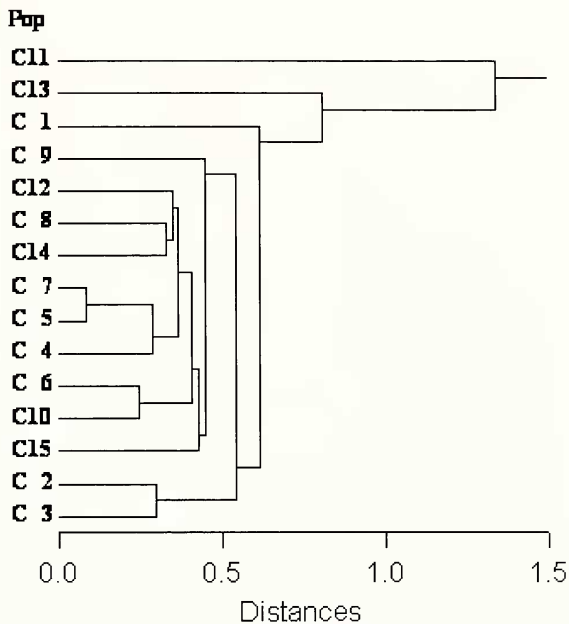


FIG. 7. Cluster analysis for Group **C** non-glandular plants with setose hairs for lower and upper bract length. See Table 1 for trait description and Table 3 for populations described by the case numbers.

California and northern Baja California. Some previous taxonomic treatments have given these two taxa status as distinct species, *A. glandulosa* Eastw. and *A. cushingiana* Eastw. We believe there are a number of traits that reflect a close relationship and a common origin, which justifies including both in *A. glandulosa*. These traits are: the basal burl, predominantly isofacial leaves, small fruits with mealy mesocarp and separable endocarp segments, and a high frequency of populations with foliaceous bracts, although

TABLE 4. FRUIT COMPARISONS BETWEEN *A. GLANDULOSA* POPULATIONS AND *A. PARRYANA* SUBSPECIES. Three populations of the former species from the interior region of the San Gabriel Mountains, Los Angeles Co. are suspected to be of hybrid origin with *A. parryana*. The range of variation in *A. glandulosa* is illustrated by the population outside this region with the smallest (B8) and largest (C5) fruits; see Table 3 for further details on *A. glandulosa* populations.

Population	Location	Fruit characters					
		Mass (mg)	Height (mm)	Width/height ratio	Endocarp segments	Single stone (%)	Apiculate (1-5)
<i>A. glandulosa</i>							
B8	Del Mar Coastal San Diego	100	4.6	1.6	4.4	0	2.8
C5	Santa Ana River San Bernardino Mtns.	373	7.6	1.3	3.2	5	3.1
B11	Glendora Ridge Interior San Gabriel Mtns.	360	8.6	1.2	2.4	32	3.7
B16	Pacific Pk Interior San Gabriel Mtns.	409	8.2	1.3	2.1	32	3.3
B19	Mill Creek Summit Interior San Gabriel Mtns.	495	9.9	1.2	2.0	35	4.0
<i>A. parryana</i>							
subsp. <i>parryana</i>	Santa Ynez Mtns. (n=58)	329	9.4	1.0	1.1	93	4.3
subsp. <i>tumescens</i>	San Bernardino Mtns(n=31)	424	10.4	1.0	1.1	97	4.2

TABLE 5. *ARCTOSTAPHYLOS GLANDULOSA* SUBSPECIES AS TREATED IN THIS STUDY ALONG WITH A BRIEF TAXONOMIC HISTORY OF THEIR TREATMENT AND SYNONYMY. See text for more details.

This treatment	As named	Date	Author	Changes in status	
subsp. <i>glandulosa</i>	<i>A. glandulosa</i>	1897	Eastwood		
		1939	Adams ex. McMinn	var. <i>glandulosa</i>	
			1968	Wells	subsp. <i>glandulosa</i>
	<i>A. intricata</i>	1901	Howell		
	<i>A. zacaensis</i>	1933	Eastwood		
		1939	Adams ex. McMinn	var. <i>zacaensis</i>	
		1968	Wells	subsp. <i>zacaensis</i>	
	var. <i>australis</i>	1940	Adams		
	<i>A. nitens</i>	1945	Eastwood		
subsp. <i>leucophylla</i>	subsp. <i>leucophylla</i>	2007	Keeley, Vasey & Parker		
subsp. <i>atunescens</i>	subsp. <i>atunescens</i>	2007	Keeley, Vasey & Parker		
subsp. <i>cushingiana</i>	<i>A. cushingiana</i>	1933	Eastwood		
		1933	Eastwood		
		1939	Adams ex. McMinn	var. <i>cushingiana</i>	
		2007	Keeley, Vasey & Parker	subsp. <i>cushingiana</i>	
subsp. <i>crassifolia</i>	var. <i>crassifolia</i>	1922	Jepson		
		1925	Jepson	<i>A. tomentosa</i> (Pursh) Lindley	
				var. <i>crassifolia</i>	
		1968	Wells	subsp. <i>crassifolia</i>	
subsp. <i>erecta</i>	subsp. <i>erecta</i>	2007	Keeley, Vasey & Parker		
subsp. <i>adamsii</i>	var. <i>adamsii</i>	1958	Munz		
		1974	Munz	subsp. <i>adamsii</i>	
subsp. <i>gabrielensis</i>	<i>A. gabrielensis</i>	1992	Wells		
		2007	Keeley, Vasey & Parker	subsp. <i>gabrielensis</i>	
subsp. <i>mollis</i>	var. <i>mollis</i>	1940	Adams		
		1968	Wells	subsp. <i>mollis</i>	
			subsp. <i>glaucomollis</i>	1987	Wells

bract size is variable in both glandular and non-glandular populations. In addition, in some parts of the range glandular and non-glandular plants form mixed populations that combine traits of both taxa, and we have the impression that such populations are more common than suspected hybrids between distinct species in the genus. Here we treat these two taxa as *A. glandulosa* Eastw. subsp. *glandulosa* (henceforth referred to as the nominate subspecies) and *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey & Parker, comb. nov. (Table 5). These taxa separate out along complex environmental gradients involving latitude, elevation and distance from the coast. In some regions their distribution is easily delineated; for example, in San Luis Obispo Co. the nominate subspecies is apparently restricted to the coastal foothills and *A. glandulosa* subsp. *cushingiana* is restricted to the higher interior ranges (Hoover 1970; J. Keeley personal observations). However, this pattern is not universal as further north from Marin Co. to Mendocino Co. the latter taxon is often found near the coast (e.g., B26 and B27). In both the glandular and non-glandular forms we find additional variation that is distinct and geographically constrained and treat these variants as additional subspecies. These, along with their taxonomic history are summarized in Table 5.

Glandular Subspecies

Most glandular populations (Group A) fall within the nominate subspecies, but two variations are recognized at the subspecies level. One is an intensely glaucous-leaved shrub that in other respects resembles the nominate subspecies (Fig. 4) and is here named *A. glandulosa* Eastw. subsp. *leucophylla* Keeley, Vasey & Parker, subsp. nov. These very white-leaved plants superficially resemble the non-glandular *A. glandulosa* Eastw. subsp. *adamsii* (Munz) Wells but have glandular hairs and most commonly have foliaceous bracts. This taxon is intensely glaucous like some of the plants in the type population of *A. zacaensis* Eastw. However, it is very unlike *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells, which was circumscribed as either glandular or non-glandular and with any degree of glaucous wax (Wells 1987, 2000a). Many populations in the southern half of the state that Wells considered to be *A. glandulosa* subsp. *zacaensis* are indistinguishable from the nominate subspecies, therefore we have purged that name from *Arctostaphylos* nomenclature. In the present study *A. glandulosa* subsp. *leucophylla* is represented by two populations, one from Cerro Bolo Peak in Baja California (A3, Fig. 4) and one from the north side of Palomar Mountain in San

Diego Co. (A16). Other populations close to this taxon (Fig. 4) and perhaps appropriately considered under this name are A14 from the east side of Palomar Mountain and A18, further west in Rancho California, Riverside Co.

A second glandular taxon that we recognize is a non-burl forming population from a mountain south of Punta Banda, Baja California, *A. glandulosa* Eastw. subsp. *atumescens* Keeley, Vasey & Parker, subsp. nov. This is a very localized population dominated by non-burl forming shrubs, probably covering only a few hectares, but in light of the near universal presence of a burl and resprouting ability in *A. glandulosa*, this unique population is considered worthy of formal recognition. The full range of this subspecies is unknown and needs further work as non-burl forming populations of *A. glandulosa* have been reported further south near San Vicente (Philip Rundel, personal communication, May 2006).

Non-Glandular Subspecies

Non-glandular taxa are characterized by short-canescens or tomentose branchlets without (Group B) or with (Group C) long villous or setose hairs. Plants lacking these long hairs are the most common non-glandular form and *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey & Parker is the most widespread of these, being found throughout the latitudinal range of the species.

In the southern part of the range we recognize four other non-glandular non-setose tomentose subspecies. One of these *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells (populations B8, B9, and B10, Fig. 5) is a long established taxon from coastal San Diego Co. Interestingly this taxon has been readily accepted by many investigators (except Eastwood and Knight), yet it has not been described in terms that are very unique within the species. Jepson (1922) delineated it on the morphological basis that it had thick leaves, a trait shared with other populations of the species, and Adams (1940) described it based on its dark green leaves, a trait that is not unique to these coastal populations of *A. glandulosa*. We believe the primary reason for its ready acceptance as a subspecies worthy of recognition is that it has a close association with coastal terraces, atypical for *A. glandulosa*, and its non-glandular branchlets, which contrasts with the nearest conspecific populations of the glandular nominate subspecies not far inland (e.g., Escondido, A10, Table 3). However, a trait largely over-looked by *Arctostaphylos* specialists (except Wiggins 1980), but evident in our analysis, is the presence of small and markedly flattened fruits. As for distribution, this taxon is restricted to within 5 (or possibly 10) km of the coast from Encinitas south into Baja California. Wells (2000a) considered this sub-

species to extend north to Carlsbad; however, our data show that many of these plants (A11) have glandular hairs, and we suggest these more northern populations represent a mixture of *A. glandulosa* subsp. *crassifolia* with the nominate subspecies. While some glandular hairs are present in the Encinitas population (B10), they only represented 5–10% of the population and our Del Mar population (B8) lacked glandular hairs.

Another non-glandular form is represented in the La Candelaria population (B1, Fig. 5) east of Ensenada, Baja California, characterized by the distinctive trait of erect nascent inflorescences. Nascent inflorescences, which persist fully formed for half a year prior to flowering, are a hallmark trait in *Arctostaphylos*; with one rare exception in *A. pringlei* (Keeley 1997, Vasey and Parker 1999, c.f. Wells 1999). In the vast majority of species these nascent inflorescences are pendant and that is the typical condition in *A. glandulosa*. The La Candelaria populations share this erect trait with two other Baja California species, *A. australis* Eastw. and *A. moranii* Wells, and the southern San Diego Co. *A. otayensis* Wieslander and Schreiber. Because this characteristic was previously unknown from *A. glandulosa*, these populations are named *A. glandulosa* Eastw. subsp. *erecta* Keeley, Vasey & Parker subsp. nov.

A non-glandular glabrous-leaved plant with highly reduced deltoid-acuminate bracts (B3, B4, B5 and B7, Fig. 5) is the subspecies originally named by Munz, *A. glandulosa* Eastw. subsp. *adamsii* (Munz) Wells. We follow the original description by Munz (1958) and reject the *sensu lato* treatment by Wells (1987, 2000a), who expanded this subspecies to include populations with glandular hairs and foliaceous bracts. In our treatment, intensely glaucous leaved plants fall into one of two subspecies, largely dependent on the presence or absence of glandular branchlets. Intensely glaucous-leaved plants with glandular branchlets, and often with foliaceous bracts, falls within *A. glandulosa* subsp. *leucophylla* Keeley, Vasey & Parker, whereas non-glandular intensely glaucous plants with highly reduced bracts are *A. glandulosa* subsp. *adamsii*.

The other non-glandular tomentose subspecies has bright green somewhat lustrous leaves, with reduced bracts and has a greater degree of nutlet fusion than in other *A. glandulosa* taxa (B11, B13, B14, B15, B16, B17, B18, B19, and B24, Fig. 6). Some individual plants produce a solid stone (Table 3), but most plants have 2–3 endocarp segments, with some individuals in all populations ranging from 1–4 segments. This taxon subsumes *A. gabrielenis* Wells, and here is treated as *A. glandulosa* Eastw. subsp. *gabrielenis* (Wells) Keeley, Vasey, & Parker, comb. nov.

Lastly, of the non-glandular forms, we recognize only one taxon with long setose or villous

hairs, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells. We do not recognize *A. glandulosa* Eastw. subsp. *glaucomollis* (Eastw.) Wells as a separate

entity due to the lack of any clear geographical distribution of foliaceous and scale-like bracts (Fig. 7) as proposed by Wells (1987, 2000a).

KEY TO *ARCTOSTAPHYLOS GLANDULOSA* SUBSPECIES

1. Branchlets with glandular hairs and bracts mostly foliaceous
 2. Leaves scabrous with non-glaucous to moderate glaucous bloom
 3. Basal burl present (Baja to Oregon) subsp. *glandulosa*
 - 3' Basal burl absent (N. Baja) subsp. *atumescens*
 - 2' Leaves with intensely glaucous bloom (interior southern California) subsp. *leucophylla*
- 1' Branchlets lacking glandular hairs, sometimes slightly viscid inflorescence
 4. Branchlets short-villous, tomentose or puberulent, leaves glabrate to moderately tomentose
 5. Leaves slightly pubescent yellow-green to dark green, lower inflorescence bracts foliaceous or reduced
 6. Nascent inflorescences pendant
 7. Fruits slightly flattened, leaves green or gray-green (Baja to Oregon) subsp. *cushingiana*
 - 7' Fruits markedly flattened, leaves dark green, leaf margins sometimes reddish (coastal San Diego Co.) subsp. *crassifolia*
 - 6' Nascent inflorescences erect (n. Baja) subsp. *erecta*
 - 5' Leaves glabrate and intensely dull white or highly lustrous green, lower inflorescence bracts mostly reduced or absent
 8. Leaves intensely glaucous, fruit endocarp 2–4 segments (interior San Diego Co. and n. Baja) subsp. *adamsii*
 - 8' Leaves bright lustrous green, fruit endocarp 1–2 segments of fused nutlets (interior San Gabriel Mountains, Sierra Madre Mountains) subsp. *gabrielensis*
 - 4' Branchlets pubescent to almost glabrate but with long setose or villous hairs, bracts variable, plants in the western portion of the range with upper leaf surface somewhat lustrous and having substantially fewer stomata than the lower surface (South Coast and Transverse ranges, occasionally further south) subsp. *mollis*

Arctostaphylos glandulosa Eastw. subsp. *glandulosa* (Eastw.) Wells, Eastwood Manzanita, Proc. Cal. Acad. Sci. ser. 3, 1:82. 1897. *A. intricata* Howell, Fl. NW. Amer., Vol. I, 417, 1901. *A. zacaensis* Eastw., Leafl. West. Bot. 1:79, 1933. *A. glandulosa* Eastw. var. *zacaensis* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *howellii* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. *A. glandulosa* Eastw. subsp. *howellii* (Eastw.) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *australis* Adams, J. Elisha Mitchell Sci. Soc. 56:51, 1940. *A. nitens* Eastw. Leafl. West. Bot. 4:148, 1945. — SYNTYPE: USA, California, Marin Co., Mt. Tamalpais, 5 March 1922, *A. Eastwood 11078* (holotype, CAS).

Evergreen shrub with pendulous nascent inflorescences appearing in the late spring and summer prior to the following winter flowering season and with a swollen basal lignotuber with dormant buds that initiate growth after fire. Isofacial leaf anatomy with well-developed palisade tissue on both sides and abundant stomata on both the upper and lower leaf surfaces, scabrous and dark green with or without light glaucous bloom, indument of short to long hairs, many with glands, nascent inflorescences usually with lower bracts foliaceous, but sometimes all bracts reduced, and depressed fruits with width

greater than height, mealy endocarp, and nutlets separable into 2–5 segments.

Distribution: Coastal mountains from northern Baja California to Oregon.

Epithet etymology: The epithet refers to the glandular hairs on branchlets, rachises, and sometimes pedicels and fruits.

***Arctostaphylos glandulosa* Eastw. subsp. *atumescens* Keeley, Vasey & Parker, subsp. nov. — TYPE: MEXICO, Baja California, north-facing slopes along dirt road between Cerro El Cantil and Cerro Buenavista, southwest of Punta Banda, 610 m, 31°40' N, 116°36' W, 26 Aug 1993, *J.E. Keeley, A. Massihi, & C.J. Fotheringham 24160* (holotype, RSA; isotypes, CAS, ENS, SD, UC).**

A. glandulosa Eastw. subsp. *glandulosa* lignotubere deficienti et non repullulans post ignem differt.

Differing from the nominate subspecies by lacking a lignotuber and not resprouting after fire.

Distribution: Type locality only confirmed location.

Epithet etymology: Refers to the lack of a basal burl, a unique characteristic in this species.

***Arctostaphylos glandulosa* Eastw. subsp. *leucophylla* Keeley, Vasey & Parker, subsp. nov. — TYPE: USA, California, San Diego Co., Heliport on northeastern face of Palomar Mountain., on road to High Point, 9.3 km**

southwest of Hwy 79, 33°20', 116°47' W, 1505 m elevation, 18 Sept 1992, *J.E. Keeley 21289* (holotype, RSA; isotypes, CAS, UCB, SD, ENS).

A. glandulosa subsp. *glandulosa* foliis glaucis maxime differt.

Differing from the nominate subspecies by extremely glaucous leaves.

Paratypes: MEXICO, Baja California, steep slopes in vicinity of Nativos de Vaille, above road to Punta Cabras, 15 km south of Santa Tomás, 400 m, 4 Aug 1993, *A. Massihi, S.A. Hiraes, & J.E. Keeley 23809* (RSA); Baja California, Cerro Bolo Peak, 1220 m, 32°19', 25 July 1993, *J.E. Keeley 23440* (RSA); USA, California, San Diego Co., along Old Ranch Rd., 1 km southwest of Hwy. 8 at Japutal Valley, 1040 m, 8 Aug. 1993, *J.E. Keeley 24038* (RSA); chaparral northwest of intersection between Japutal Valley Rd. and Lawson Truck Trail, 700 m, 6 Sept 1975, *J.E. Keeley 5879* (RSA); along Mother Grundy truck trail, 1 km south of Honey Springs Rd., 600 m, 8 Aug. 1993, *J.E. Keeley 24013* (RSA); Los Pinos Peak, northwest of Lake Moreno on 16S17, 1460 m, 8 Aug 1993, *J.E. Keeley 24060* (RSA); north-facing slope of Guatay Peak, 1120 m, 8 Aug 1993, *Keeley 24,051* (RSA); Flinn Ranch (Kitchen Creek) Rd., 15 km north of Old Hwy 80, southern Laguna Mountains., 1590 m, 17 Aug 1992, *J.E. Keeley, A. Massihi, & R. Gore 18906* (RSA); Riverside Co., rock outcrop Red Mountain. Rd./Stanely Rd., 11.7 km east of R3, 975 m, 16 July 1992, *J.E. Keeley 16587* (RSA); Hwy 234, 3 km north of Hwy 74, San Jacinto Mountains., 1520 m, 16 June 1992, *J.E. Keeley 16819* (RSA).

Distribution: Away from the coast often on gabbro or basaltic soils in southern California and northern Baja California.

Epithet etymology: This epithet refers to the intensely white glaucous leaves.

Arctostaphylos glandulosa* Eastw. subsp. *cushingiana (Eastw.) Keeley, Vasey & Parker, comb. nov. *A. cushingiana* Eastw., Leafl. West. Bot. 1:75, 1933. *A. howellii* Eastw., Leafl. West. Bot. 1:123, 1934. *A. glandulosa* Eastw. var. *cushingiana* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. — TYPE: USA, California, Marin Co., south side of Mt. Tamalpais, 12 March 1922, *A. Eastwood 11075A* (holotype, CAS).

Lacking glandular hairs. Branchlets with short hairs, puberulent or tomentose. Occasional populations included here may have glands on inflorescences and/or fruits.

Distribution: From northern Baja California to northern California (perhaps Oregon). In the south mostly on interior sites.

Epithet etymology: This epithet honors Sidney Cushing, someone "who during his life, identified with Mount Tamalpais" (Eastwood 1933).

Arctostaphylos glandulosa Eastw. subsp. *crassifolia* (Jepson) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *crassifolia* Jepson, Madroño 1:86, 1922. *A. tomentosa* (Pursh) Lindley var. *crassifolia* (Jepson) Jepson, Manual fl. Plants Calif. 749, 1925. — TYPE: USA, California, San Diego Co., sandy mesas at Del Mar, 9 June 1901 *W.L. Jepson 1606a* (holotype, UC).

Lacking glandular hairs. Branchlet and nascent indument tomentose to short villous. Leaves dark green, sometimes with a reddish margin. Fruits markedly more flattened than other subspecies.

Distribution: Coastal sandstone substrates from north of Encinitas in San Diego County south to near Erendira, Baja California.

Epithet etymology: The epithet recognizes the somewhat thicker leaves on this taxon.

Arctostaphylos glandulosa* Eastw. subsp. *erecta Keeley, Vasey & Parker, subsp. nov. — TYPE: MEXICO, Baja California, foothills 32 km east of Ensenada in foothills along Hwy 3, 600 m, 31°53' N, 116°19' W, 24 July 1992, *J.E. Keeley, A. Massihi, & R. Goar 17927* (holotype, RSA; isotypes, CAS, ENS, SD, UC).

Trichomata glanduliferis deficientia. Ramuli tomentosi. Inflorescentiae nascentes erectae.

Glandular trichomes absent; branchlets tomentose. Nascent inflorescences erect.

Distribution: Foothills at the southwestern end of the Sierra Juarez Mountains in northern Baja California.

Arctostaphylos glandulosa Eastw. subsp. *adamsii* (Munz) Munz, Flora S. Calif. 400, 1974. *A. glandulosa* Eastw. var. *adamsii* Munz, Aliso 4:95, 1958. — TYPE: USA, California, San Diego Co., northern end of the Laguna Mtns. along road to Julian, 20 Aug 1942, *P.A. Munz & E.K. Balls 17958* (holotype, RSA).

Lacking glandular hairs or other long hairs, branchlets tomentulose to tomentose. Leaves glabrous, dull and densely glaucous. Nascent bracts reduced deltoid.

Distribution: Interior edge of chaparral in San Diego County south into interior northern Baja California.

Epithet etymology: This epithet honors J.E. Adams, one of the important 20th century students of the genus and whose Ph.D. dissertation was the standard treatment for *Arctostaphylos* during most of the latter two-thirds of the century.

Arctostaphylos glandulosa Eastw. subsp. **gabrielensis** (Wells) Keeley, Vasey & Parker, comb. nov., *A. gabrielensis* Wells, Four Seasons 9(2):46–47, 1992. — TYPE: USA, California, Los Angeles Co., San Gabriel Mountains, Mill Creek Summit, 1470 m, 10 March 1986, *P. V. Wells & J.E. Keeley 31086* (holotype, CAS).

Lacking glandular hairs, branchlets tomentulose, leaves glabrous, lustrous and bright green. Nascent bracts reduced deltoid and fruits similar to the nominate subspecies in shape but larger often reddish pericarp and more leathery mesocarp and with a tendency for nutlets to coalescence into 1–2 (4) segments of one or more drupelets.

Paratypes: USA, California, Los Angeles, Co, Glendora Ridge Rd., 6 km southwest of Baldy Rd., 1410 m, 15 Oct 1992, *J.E. Keeley & M.B. Keeley 22122* (RSA); Singing Pines Camp, Angeles Crest Hwy, 2000 m, 2 Sept 1978, *J.E. Keeley 7226* (RSA); south-facing slopes at end of Hwy 39, northwest of Crystal Lake, 1720 m, 15 Oct 1992, *J.E. Keeley 22101* (RSA); Santa Barbara Co., Sierra Madre Rd, 13 km west of McPherson Peak, Sierra Madre Mountains, 1690 m, 7 Aug. 1992, *J.E. Keeley & M.B. Keeley 19017* (RSA).

Distribution: Mostly interior portions of the San Gabriel Mountains, Los Angeles Co., occurring in disjunct populations as far north as the Sierra Madre Mountains, Santa Barbara Co.

Epithet etymology: The epithet reflects the distribution of this subspecies is largely in the San Gabriel Mountains.

Arctostaphylos glandulosa Eastw. subsp. *mollis* (Adams) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *mollis* Adams, J. Elisha Mitchell Sci. Soc. 56:50, 1940. *A. glandulosa* Eastw. subsp. *glaucomollis* Wells, Four Seasons 7(4):20, 1987. — TYPE: USA, California, Santa Barbara Co., La Cumbre Peak, Santa Ynez Mountains, 20 Feb 1935, *J.E. Adams 954* (holotype, UC).

Lacking glandular hairs. Branchlets with short hairs, puberulent or tomentose and with long villous hairs. Occasional populations included here may have glands on inflorescences and/or fruits. Throughout the range bract size varies from foliaceous to reduced.

Distribution: South Coast and Transverse ranges and occasional populations in the Peninsular Ranges and coastal mountains of San Diego and Baja California.

Epithet etymology: Refers to the long soft flexible hairs.

DISCUSSION

Arctostaphylos glandulosa Eastw. is a wide ranging tetraploid species circumscribed as hav-

ing isofacial leaves with stomata on both leaf surfaces, indument with short or long hairs, glandular or non-glandular branchlets, pendant nascent inflorescences, depressed-globose fruits usually with separable endocarp segments of several nutlets, and a basal burl. This study has shown that there is some population level variation in many of these traits, including populations with markedly bifacial leaves, or with erect nascent inflorescences, or a tendency towards solid stones and even one population lacking a basal burl. Many of these population level characteristics vary in geographically predictable patterns and should be given taxonomic recognition.

Subspecific variation is dominated by two widely distributed morphotypes, the glandular nominate subspecies and the non-glandular short pubescence *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey and Parker. In addition, seven other subspecies of more localized distribution are recognized, largely concentrated in southern California and Baja California. These subspecies are based on phenetic patterns of variation and represent relatively monomorphic allopatric populations. Where these taxa meet, mixed populations may occur.

Any taxonomic treatment assumes that all populations of a given taxon have a common origin. In highly localized subspecies of *A. glandulosa* there is far less reason to question that assumption than for wide ranging subspecies, some of which require critical evaluation. For example, Wells (1987, 2000a) considered any level of glaucous bloom on leaves of plants from central and southern California constituted *A. glandulosa* subsp. *zacaensis* and the origin of this trait was due to hybridization with *A. glauca*. However, Wells' circumscription of *A. glandulosa* subsp. *zacaensis* comprised a wide diversity of populations with slight to moderate glaucous bloom, over a huge distributional range. Here we do not recognize that taxon because the presence of any amount of glaucousness on the leaf is potentially a trait of diverse origins throughout the range. The numerous demonstrated cases of hybridization in *Arctostaphylos* (Dobzhansky 1953, Howell 1955, Gottlieb 1968, Keeley 1976, Kruckeberg 1977, Ellstrand et al. 1987), and the number of intensely glaucous-leaved species found throughout the range that could be potential contributors to the glaucous foliage, provide justification for questioning that taxon. This decision also eliminates major problems in correctly classifying many populations within the range Wells (1987, 2000a) circumscribed for *A. glandulosa* subsp. *zacaensis*. For example, all glandular plants south of San Francisco were considered to be this taxon yet our analysis revealed three populations (A12, A13, and A6, Fig. 4) in southern California that were distinctly non-glaucous.

Understanding patterns of variation in *A. glandulosa* requires some evaluation of the palaeohistory of vegetation distribution in this region. Over most of the last 2 million years conditions throughout the area now characterized as the California Floristic Province were cooler and wetter than today, and thus the contemporary plant distribution is not likely more than 10,000 years old. Prior to this many chaparral taxa such as *Arctostaphylos* were distributed much further south or lower in elevation (Axelrod 1950; Raven and Axelrod 1978; Wells 2000b; Rhode 2002). Holocene climate changes resulted in migration that followed unique patterns for different taxa, potentially bringing together populations long isolated from one another. These conditions likely set the stage for potential hybridization and introgression of genetic variation from previously isolated *Arctostaphylos* taxa and form the basis for Wells (2000a) model of "reticulate evolution" in the genus. While many aspects of this model are likely true, it tends to downplay the potential role for strong directional selection under the changing climatic conditions of the Holocene. These two models of course are not mutually exclusive and likely have worked in concert to generate contemporary patterns of subspecific variation in *A. glandulosa*.

The role of hybridization has been considered by Wells (2000a) to have been of immense importance in the evolution of *Arctostaphylos* and he speculated on numerous hybridization events involving *A. glandulosa*. Several factors complicate such evaluations. Claims of hybridization by Wells (2000a) were based on the presence of shared traits and often unwarranted assumptions about the direction of gene transfer from one taxon to another. In addition these hybrid claims were markedly influenced by the current overlap in species ranges. This latter factor is particularly troubling because of the distinct possibility that the origin of subspecific variation within *A. glandulosa*, or any other species, may not be recent, and some of it could predate the current distribution patterns of related taxa. For example, Wells (1987, 2000a) claimed that *A. campbellae* was a hybrid between *A. crustacea* and *A. glauca*, but based on patterns of phenetic variation (Fig. 2) there is good reason to discount involvement of the latter species in the origin of *A. campbellae*. Indeed, if hybridization were involved, patterns of morphological similarity would favor *A. glandulosa* as one of the parents (Fig. 2). Apparently the presence of *A. glauca* in the vicinity and absence of *A. glandulosa* from the region led to Wells' unlikely conclusion about the origin of *A. campbellae*. Of course there is no reason to *a priori* assume hybridization is the driver behind this particular taxon and an equally plausible hypothesis is that directional

selection in *A. crustacea* has selected for decreased bifaciality of leaves and other changes of selective value on the drier more interior slopes of Mt. Hamilton and San Antonio Valley in Santa Clara County. This directional selection model may be what McMin (1939) and Adams (1940) had in mind when they hypothesized that *A. crustacea* was a likely intermediate stage between the coastal *A. tomentosa* and the interior *A. glandulosa*. Consistent with this model is the morphological similarity of *A. campbellae* and *A. glandulosa* subsp. *mollis*; similar in that both are non-glandular with long villous hairs. These taxa differ largely in their relative placement on a scale from bifacial to isofacial leaves, with the latter taxon falling somewhere between *A. campbellae* and other *A. glandulosa* subspecies.

Future molecular studies may help resolve some of the unknowns about the origins of variation in *Arctostaphylos glandulosa*. However, interpreting both morphological and molecular data will require a better understanding of how to detect pathways of reticulate evolution resulting from hybridization and introgression and how to distinguish this from directional selection along environmental gradients.

CONCLUSIONS

This study clarifies some ambiguity and confusion in the most recent classification of subspecific variation in *A. glandulosa* (Wells 2000a). In our treatment the nominate subspecies has been restored as the dominant glandular taxon throughout the range of the species. A new combination was made to include most non-glandular pubescent populations, *A. glandulosa* subsp. *cushingiana*. Two subspecies, *A. glandulosa* subsp. *crassifolia*, and *A. glandulosa* subsp. *adamsii*, which had been re-described by Wells to circumscribe a wider range of variation, were returned to taxa more closely approximating the type specimen. This treatment of the latter taxon required describing a new subspecies, *A. glandulosa* subsp. *leucophylla*, for glandular plants with intensely glaucous leaves. One species, *A. gabriellensis* was subsumed under *A. glandulosa* subsp. *gabriellensis*. The former subspecies *A. glandulosa* subsp. *glaucomollis* was subsumed under *A. glandulosa* subsp. *mollis*. Two new localized subspecies from Baja California are named, *A. glandulosa* subsp. *atumescentes*, similar to the nominate subspecies but is a uniquely non-burl forming taxon, and *A. glandulosa* subsp. *erecta*, a non-glandular taxon with erect nascent inflorescences.

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